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# Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats

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ABSTRACT: Food selection by the Caribbean stoplight parrotfish *Sparisoma viride* was investigated on a fringing coral reef of Bonaire, Netherlands Antilles. For different reef zones, the diet composition for each life phase was determined by description of randomly selected bites, and compared to the availability of food resources, as determined with the aid of chain-link transects. *S. viride* employs an excavating grazing mode, and feeds almost exclusively on algae associated with dead coral substrates. Preferred food types are large and sparse turfs growing on carbonate substrates inhabited by endolithic algae. Crustose corallines, with or without algal turfs, are not preferred. Feeding forays were longer on the preferred food types. Foraging preferences are related to nutritional quality of the food types and their yield, i.e. the amounts of biomass, protein and energy that can be ingested per bite, as calculated from the size of grazing scars and the biochemical composition of the algae. In spite of selective foraging, a large proportion of bites is taken on inferior food types. Endolithic algae constitute an important food resource for scraping herbivores, such as *S. viride*. These algae have relatively high energetic value, and allow a high yield as a result of weakening the carbonate matrix by their boring filaments. The yield of algal resources also depends on the skeletal density of the limestone substrates. On deeper reef parts (>3.5 m depth), low-density substrates predominate, resulting in higher yields of algae per bite than are attained from high-density substrates that predominate on shallower reef parts. The increased availability of high-yield food and substrate types coincides with the occurrence of haremic territorial behaviour in *S. viride* males on the deeper reef parts. Territories are defended against conspecifics and have an important function as spawning sites. It is argued that the access to superior food resources on the deeper reef makes territorial defence feasible for *S. viride*.

KEY WORDS: Coral reefs · Herbivory · Scaridae · Diet · Food quality · Territorial defence · *Sparisoma varide*

## INTRODUCTION

Coral reefs support an abundant and diverse population of herbivores, including microcrustaceans, molluscs, echinoids and fish (Hiatt & Strasburg 1960). On reefs subject to minimal human disturbance, herbivorous fish in the families Acanthuridae (surgeonfish) and Scaridae (parrotfish) are the predominant herbivores, both in terms of population density and algal biomass consumed (Randall 1965, Lewis & Wainwright 1985, Lewis 1986). Although the importance of scarids in bioerosional processes on coral reefs has long been acknowledged and quantified (Gygi 1975, Ogden 1977, Frydl & Stearn 1978, Kiene 1988), surprisingly little is known about their role in the flow of energy in the coral reef food web (Horn 1989).

Given the low levels of protein and energy in benthic algae, herbivorous fish might be expected to choose algae high in nutritional quality (Horn 1989). Except for the findings of some more general field experiments on food choice in tropical herbivores, including parrotfish (Hay et al. 1987), little is known about diet selection by parrotfish in natural situations (Horn 1989). The work of Lobel & Ogden (1981) on the Caribbean *Sparisoma radians*, in which experimental work and field observations were combined to evaluate foraging selectivity, forms a notable exception. Other field studies, including algal transplant experiments (Lewis 1985, 1986) and experiments to assess the role of algal secondary compounds, have shown that scarids are selective feeders. These studies have focused on selectivity for individual algal taxa as

related to the occurrence of chemical feeding deterrents. In natural situations, however, large herbivorous fish are confronted with a multispecies array of food plants, most of which are too small to be selected individually (Choat 1991). Moreover, food selection in the field is determined by the availability of resources, and subject to social constraints such as territorial behaviour by conspecifics or other species.

This study is part of a larger project aiming to evaluate the role of parrotfish, in particular the stoplight parrotfish *Sparisoma viride* (Bonnaterre), in the trophodynamics of coral reefs. *S. viride* is a large generalist herbivore that is common on Caribbean coral reefs from Bermuda to Brazil (Randall 1968). It forages by scraping and excavating epilithic and endolithic algae from the carbonate substrates. Although fish can cover all reef zones in daily migrations, foraging of individuals is restricted to certain reef areas as a result of the social structure of *S. viride* (Cardwell 1989, J. M. van Rooij, F. Kroon & J. J. Videler unpubl.). Territories defended by single males are found only in deeper reef zones, whereas large numbers of non-territorial fish feed on the shallow reef.

In this study we attempt to answer the following questions: (1) To what characteristics of a food item is selective foraging related? (2) Is the social organization in *Sparisoma viride* related to the availability of food resources in different reef zones?

## METHODS

**General description of study area.** The study was performed at Karpata (12° 13' N, 68° 20' W), which is part of a continuous fringing reef on the leeward side of Bonaire, Netherlands Antilles (Fig. 1A). Seawater temperatures range from 26 to 29°C throughout the year. The mean daily sunshine percentage is 67.6% and varies only slightly during the year; days without clouds and entirely cloudy days are rare on the Netherlands Antilles (Wanders 1976). The waters around the island were designated a marine park in 1979, and anchoring on the reef, as well as spearfishing, has since been banned. Parrotfish are abundant on the reefs of Bonaire. As they are not shy, behavioural observation at close range (< 1 m) was possible.

At the study site several reef zones (Fig. 1B) characteristic of Caribbean coral reefs can be distinguished along a depth gradient (Bak 1975, 1977, van den Hoek et al. 1975, 1978, Wanders 1976):

The reef crest (0 to 0.3 m depth, ca 4 m wide) is a limestone plateau formed by dead *Acropora palmata* coral, amalgamated by crustose coralline algae, predominantly *Porolithon pachydermum* (van den Hoek et al. 1975). It is exposed at low spring tides, while

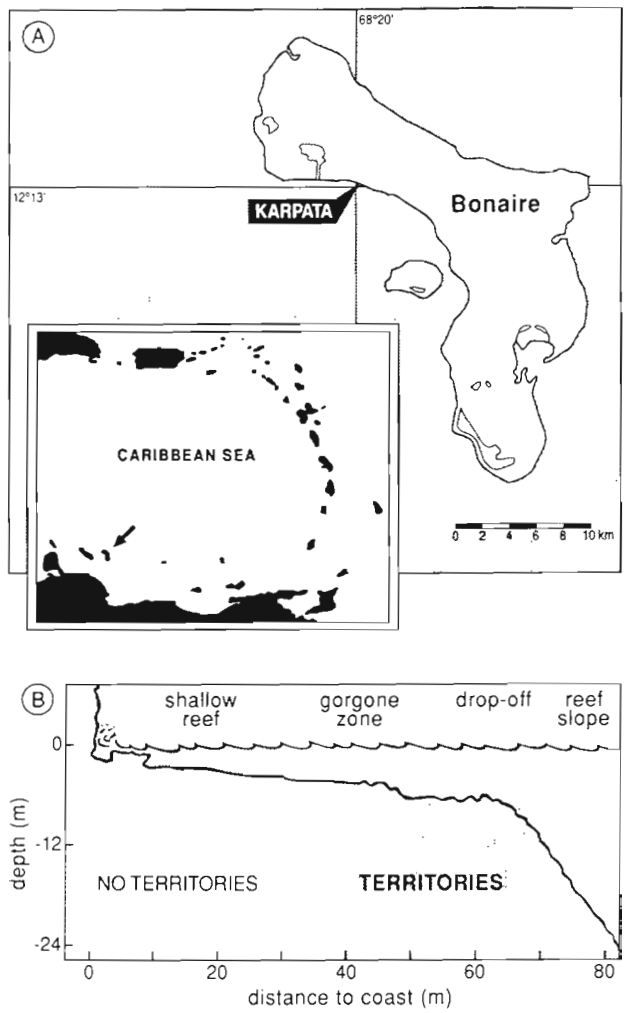



Fig. 1 (A) Map of the Netherlands Antilles in the southern Caribbean Sea, and location of study site Karpata on the leeward fringing reef of Bonaire, Netherlands Antilles. (B) Profile of the reef at the study site, and zones with territories of *Sparisoma viride* (shaded areas)

wave action excludes access by herbivorous fish at most high tides.

The shallow reef zone (0.3 to 3.5 m depth, ca 20 m wide) consists mainly of coarse rubble from the coral species *Acropora palmata* and *A. cervicornis*. Cover of living corals is low, resulting from tropical storms that hit the island in 1986 and 1988.

The dominant aspect of the gorgone zone (3.5 to 6 m depth) is the fossil carbonate platform, extending ca 60 m seaward, which is covered with a thin layer of unconsolidated limestone sediments. Large amounts of fine coral rubble bear testimony of once extensive stands of *Acropora cervicornis* coral, which died in 1980 from white band disease (Bak & Criens 1981, van Duyl 1985). A diverse gorgone fauna is characteristic for this reef zone. On the deeper parts of the platform,

cover of living coral colonies increases, notably by the coral species *Madracis mirabilis*.

The drop-off and upper reef slope (6 to 25 m depth) have the highest diversity and cover of living corals. Coral growth is dominated by *Montastrea annularis* and other massive species, which gradually changes to dominance of blade forms such as *Agaricia agaricites* deeper along the reef slope.

Below 25 m depth, cover of living corals declines while cover of fleshy algae increases. The algal vegetation is dominated by the macroalga *Lobophora variegata*.

**Reef description.** All field observations were made between February 1989 and April 1990 using SCUBA, while notes were recorded on PVC sheets. The abundance of substrates with associated biota in each reef zone was quantified in spring 1989 (March to May) using chain-link transects (Porter 1972). Sites were chosen randomly, and at each site transects were described, both parallel and perpendicular to the coast. In each reef zone, species-area curves for corals and other main bottom components were used to determine the minimum number of sample sites needed to obtain the maximum number of species. Sample sizes were chosen accordingly. In each transect, a chain consisting of 150 links of 1 cm diameter was laid out, closely following the contours of the substrate. Substrate type and biota under each link were noted. Care was taken to describe only those surfaces that were accessible to an average-sized parrotfish (ca 20 cm fork length, FL, measured from the tip of the upper jaw to the end of the middle caudal rays). Non-algal biota were identified to the species level and subsequently grouped in 2 categories: living corals and other biota (gorgonians, anemones, tunicates, etc.). Algal vegetation was divided into categories, based on the height of the epilithic algal fronds, and on the type of undergrowth of the algal community (endolithic algae or crustose corallines). Algal categories are: macroalgae (fronds >15 mm in height); large turfs (fronds 3.5 to 15 mm); sparse turfs (fronds 0.1 to 3.5 mm) growing on substrates containing endolithic algae; sparse turfs growing on crustose corallines; bare coralline crusts; and sedimented algal turfs (of all frond heights). Patches of substrate containing endolithic algae but devoid of algal turfs were never found, while the undergrowth of large turfs consisted mainly of endolithic algae. Within the main feeding ranges of *Sparisoma viride*, cover of macroalgae was low (always <1% of accessible substrates), and macroalgae such as *Dictyota* spp. were often found within large turfs. Therefore, macroalgae and large turfs were lumped into 1 category. Whenever possible, the coral origin of substrates was identified to the species level from the shape and structure of the rock. Along each transect, the surface index (*SI*), defined as the ratio of accessible substrate to that of a plane with similar boundaries (Dahl 1973), was determined.

Algal species composition in the food types grazed upon most often by *Sparisoma viride* (i.e. large turfs and sparse turfs) was investigated using samples from a variety of sites that appeared typical for the different reef zones. In the laboratory, the epilithic algae were scraped from four 1 $cm^2$ areas, selected randomly from surfaces with homogenous vegetation, using an overlying coordinate grid. Species abundance was quantified using the method described by Hackney et al. (1989). For identification of the algae, the taxonomic works of Børgesen (1913–1920) and Taylor (1960) were consulted. Jaccard's Coefficient of Community (*CC*) (Goodall 1973), based on presence or absence of algal taxa, was used to compare species composition of large and sparse algal turfs in different reef zones. Similarity values for all possible sample pairs within a reef zone were computed, after which the mean within-food-types similarity was compared to the mean between-food-types similarity using Student's *t*-test (Norusis 1990).

**Study animal.** *Sparisoma viride* is a protogynous hermaphrodite (Reinboth 1968), and shows full sexual dichromatism (Robertson & Warner 1978). In the field, 3 life phases can be distinguished, according to reproductive behaviour and colouration. These are: juveniles (JU: <15 cm FL); initial phase fish, mostly females (IP: 15 to 35 cm FL); and terminal phase males (TP: 18 to 43 cm FL). JU and IP fish are coloured a mottled brown with a red belly, while the TP males have a vivid green colour with a yellow spot on the tail base.

On the shallow reef, where fish density is highest, loosely associated groups of IP and TP *Sparisoma viride* are found. On the deeper reef (3.5 to 25 m depth) permanent territories are maintained and fiercely defended against conspecifics by single TP males (sometimes assisted by haremic IP fish). Inside territories a harem of 3 to 7 IP fish is found with which the TP male spawns daily (pers. obs.). A detailed description of the social structure and mating systems at the study site is given by van Rooij et al. (unpubl.). *S. viride* is active only by day, when it spends 70 to 90% of the time foraging (Hanley 1984, van Rooij & Bruggemann pers. obs.). At night the fish remain quiescent on the bottom, often hidden under coral boulders at sites within their feeding area, but also as far as 500 m away. Daily movements of individual fish encompass different reef zones. The size of daytime feeding areas ranges from 250 to 800 $m^2$, depending on size and social status of the fish (van Rooij et al. unpubl.).

**Field description of individual bites and of foray size.** Food choice was monitored from February to April 1989, approximately the same period during

which food availability was quantified. Individual fish were selected upon sight and allowed several minutes to become accustomed to the observer, after which 1 bite was described. Bites were selected randomly by deciding in advance which of the subsequent bites was to be described. The percentage cover of algal food types was estimated to the nearest 10% at the precise location of the bite, as was 'microhabitat' type. Two microhabitat types were distinguished: flat and convex surfaces. Coral origin of the substrate, reef zone, depth, life phase and FL (estimated to the nearest cm) of the fish were noted. The similarity of frequency distributions of algal food and dead coral substrate types in the diets of different life phases was tested with Chi-square (Norusis 1990), controlling for reef zone. If not statistically different, data were pooled and tested against the frequency distribution of food and substrate types present in each reef zone.

Additional data on food selection were collected by description of forays during August to November 1989. A foray is defined as a feeding event of successive bites without discernible interval, other than that necessary to reapply the jaws to the substratum (Bellwood & Choat 1990). Individual fish were selected upon sight, after which 1 foray was selected randomly as described above. Foray size, i.e. the number of successive bites in a foray, was recorded in relation to fish size, life phase, food type, coral origin of substrate, and foraging depth. For the variables food type, skeletal density of substrates and foraging depth, similarity of frequency distributions of total bites by foray size was tested with Chi-square.

**Size of grazing scars.** Two methods were used to quantify the surface area removed, and the volume of substrate excavated per bite from the size of scars left by grazing fish. The first method encompassed field description of bites (n = 331). With a sliding caliper, the greatest length ($L_{max}$), width ($W_{max}$) and depth ($D_{max}$) of the grazing scars were measured. Substrate surface area ($SA_{max}$) and volume ($VO_{max}$) removed per bite were calculated as:

$$SA_{max} = L_{max} \times W_{max}, \quad (1)$$

$$\text{and } VO_{max} = SA_{max} \times D_{max} \quad (2)$$

These bite sizes are an overestimation, since only the greatest length, width and depth of scars were recorded because of observational limitations in the field. The second method was used to arrive at a more accurate estimate of bite size. Substrates bearing scars caused by grazing fish of 30 cm FL (n = 50) and 36 cm FL (n = 50) were randomly selected in the field, collected with chisel and hammer, and transferred to the laboratory. First, $L_{max}$, $W_{max}$ and $D_{max}$ of grazing scars were determined, and $SA_{max}$ and $VO_{max}$ calculated as described above. To determine the real surface area removed per bite ($SA$), scars were projected at 6× magnification using a dissecting microscope with drawing mirror. The outline of a scar was traced on heavy-duty aluminum foil of known weight, which was cut out and weighed. The real substrate volume removed per bite ($VO$) was determined by taking 10 depth measurements scattered evenly over a grazing scar. $SA$ and $VO$ are calculated as:

$$SA = \text{weight of foil/specific weight of foil (g cm}^{-2}), \quad (3)$$

$$\text{and } VO = SA \times \text{mean depth of scar} \quad (4)$$

Correction factors were then calculated as $SA/SA_{max}$ and $VO/VO_{max}$.

Analysis of variance (ANCOVA, regression approach; Norusis 1990) with food type, substrate density and substrate microhabitat as main effects, and $FL^2$ or $FL^3$ as covariate of $SA$ and $VO$ respectively, was used to investigate factors affecting bite size. Data were transformed (square root of $SA$, cube root of $VO$) to meet conditions of normality and homogeneity of variances.

Skeletal density of substrates (g cm$^{-3}$) was determined from sample blocks that were cut with a diamond gem-saw from known coral species (living and dead). Blocks, dried to constant weight (for several months) at 60°C, were weighed to the nearest mg. Volume was determined by water displacement, after coral pores had been sealed off with petroleum jelly.

**Biochemical composition and yield of food types.** To evaluate the nutritional value of algal food items, we used 4 parameters: biomass, protein content, energy content and the yield per bite. For determinations of biomass [in mg ash-free dry wt (AFDW) cm$^{-2}$], pieces of substrate grown with one of the food types described above were collected from the reef, using hammer and chisel. Homogeneous patches were cut out with a diamond gem-saw. Epilithic algae were removed with a scalpel, taking care that no crustose corallines or endolithic algae were removed as well. The surface area of the sample was determined by carefully modelling heavy-duty aluminium foil of known weight over the substrate, and weighing this after drying at 60°C. After this, the undergrowth consisting of crustose corallines and/or endolithic algae was removed with a chisel, until a completely white substrate was left. Samples were dried to constant weight at 60°C (dry wt), weighed and ground to a fine powder with pestle and mortar. Immediately before analysis, samples were redried, and the organic fraction (% AFDW) was determined by weighing and reweighing duplicate subsamples after ashing at 500°C for at least 6 h (Paine & Vadas 1969).

Protein content (in mg g$^{-1}$ algal AFDW) was determined from duplicate subsamples using a modification of the method of Lowry et al. (1951). The procedures described by Montgomery & Gerking (1980) were fol-

lowed. To determine protein concentrations, absorbances were read at 750 nm with a Vitatron universal photometer (model UPM), or with a Hach spectrophotometer (model DR3000), and a bovine gamma globulin standard curve was used as a protein reference.

The energy content (in kJ $g^{-1}$ algal AFDW) was calculated from C and N weight fractions measured in a Carlo Erba Elemental Analyzer, using a modification of the stoichiometric method described by Gnaiger & Bitterlich (1984). After weighing, but prior to analysis, samples were decalcified with a solution of 0.1 N $H_2SO_3$ in water to remove inorganic C. The C and N contents were determined as a percentage of sample dry wt, and converted to percentage of AFDW using the organic fraction determined by ashing. It was assumed that 6% of algal AFDW was residual water (Gnaiger & Bitterlich 1984).

The potential yield of biomass, protein and energy per bite from different food types was calculated from the surface area of grazing scars and from the biochemical composition of the food. Estimates of the yield per bite were made for fish of 30 cm FL, and it was assumed that all algal material that was scraped off the dead coral substrates was actually ingested. By relating the total food intake per bite (Bruggemann et al. 1993) to the surface area of bite scars, and to the biomass of epilithic and substrate-bound algal fractions (endolithic algae and crustose corallines), it was inferred that on average 25% of the biomass of substrate-bound algae present under the surface area of a bite scar is harvested by a fish of 30 cm FL.

## RESULTS

### Reef description

The assemblage of reef biota differs with reef zone (Table 1). The percentage cover of large turfs and macroalgae, living corals and other biota increases along a depth gradient, while sparse turfs on endolithic algae and crustose corallines, with or without algal turf, have the highest abundance on the shallow reef. Bare sandy bottoms, without conspicuous algal biota, are characteristic of the gorgone zone.

An inventory of algal taxa present in turfs which constitute the main food types for *Sparisoma viride* (see below) shows that representatives of the 5 major taxonomic divisions are found in the food (Table 2). Based on Jaccard's *CC*, no significant difference in species composition is found between large and sparse turfs from the shallow reef zone ($CC_{\text{within sample pairs}} = 0.505 \pm 0.124$; $CC_{\text{between sample pairs}} = 0.456 \pm 0.119$; $p = 0.290$). In the gorgone zone the species composition of large turfs differs significantly from that of sparse turfs ($CC_{\text{within sample pairs}} = 0.535 \pm 0.131$; $CC_{\text{between sample pairs}} = 0.460 \pm 0.074$; $p < 0.05$). Large turf vegetation in this reef zone is often located between coral boulders, the favourite sites of territorial damselfish.

### Diet selection by *Sparisoma viride*

*Sparisoma viride* feeds virtually exclusively on algae. More than 95% of the recorded bites were taken on algal biota associated with dead coral substrates, while 31 bites (3.6%) were taken from living corals, and 4 (0.5%) from other non-algal biota. Bites on bare sandy bottoms were never observed, while bites on sedimented algal turfs were rare (0.2%).

The occurrence of the major food items (including living corals) in the diet of 3 life phases of *Sparisoma viride* is compared by reef zone in Table 3. Only on the deeper reef does the diet of JU fish differ significantly from that of IP and TP fish, with no significant differences in diet between IP fish and TP males. Therefore, bites recorded from different life phases

Table 1. Relative abundance of substrates, and their percentage cover of algal and non-algal biota, accessible to an average-sized parrotfish (ca 20 cm fork length, FL, measured from the tip of the upper jaw to the end of the middle caudal rays). Relative abundance was determined as the percentage of the total number of chain-links of n transects described in each reef zone. *SI*: surface index, ratio of accessible substrate to that of a plane with similar boundaries (Dahl 1973)

| | Dead coral substrates | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Large turfs + macroalgae | Sparse turfs on endolithic algae | Sparse turfs on crustose corallines | Crustose corallines | Sedimented algal turfs | Other biota | Living coral | Sandy bottom | No. of chain-links | *SI* ± SD (n transects) |
| Shallow reef | 3.0 | 19.3 | 46.1 | 16.1 | 3.4 | 1.2 | 10.6 | 0.3 | 4500 | 1.44 ± 0.38 (29) |
| Gorgone zone | 6.0 | 7.5 | 24.9 | 4.9 | 11.6 | 2.7 | 23.8 | 18.6 | 6287 | 1.35 ± 0.24 (39) |
| Drop-off + reef slope | 7.7 | 4.2 | 26.7 | 10.1 | 3.1 | 5.0 | 37.5 | 5.7 | 11613 | 2.09 ± 0.70 (77) |

Table 2. Relative abundance of algal taxa present in epilithic turf vegetation. Abundance scores from 150 grid intersections per sample: D = dominant, D ≥ 10 %; P = present, 10 % > P ≥ 1 %; S = scarce, 1 % > S ≥ 0.1 %; R = rare (R < 0.1 %). Unid.. unidentified

| Taxa | Shallow reef zone | | Gorgone zone | | Drop-off + reef slope |
|---|---|---|---|---|---|
| | Large turfs | Sparse turfs | Large turfs | Sparse turfs | Large turfs |
| No. of samples: | (5) | (3) | (4) | (4) | (7) |
| Cyanophyta | | | | | |
| Cyanobacteria spp. | S | P | P | P | D |
| Chlorophyta | | | | | |
| *Caulerpa vickersiae* | S | | P | P | P |
| *Cladophora* spp. | P | P | P | P | P |
| *Cladophoropsis* sp. | S | R | S | | R |
| *Enteromorpha ligulata* | P | P | S | R | R |
| *Neomeris annulata* | R | | | | |
| *Struvea anastomosans* | | | S | S | S |
| *Ulva* sp. | S | | | | |
| Unid. noncellular greens | P | P | P | P | P |
| Unid. cellular greens | R | P | | P | P |
| Bacillariophyceae | | | | | |
| Pennate diatoms | | R | S | R | R |
| Phaeophyta | | | | | |
| *Dictyota* spp. | | | | P | P |
| *Lobophora variegata* | R | | | | R |
| *Sphacelaria* sp. | P | D | P | D | P |
| Rhodophyta | | | | | |
| *Acrochaetium* sp. | P | | P | R | R |
| *Antithamnion* sp. | | S | R | | S |
| *Bryopsis pennata* | S | | | | |
| *Callithamnion* sp. | S | | | | S |
| *Centroceras clavulatum* | P | S | P | P | S |
| *Centroceras* sp. | R | | | | S |
| *Ceramium nitens* | P | P | S | R | S |
| *Ceramium* spp. | P | S | P | P | P |
| *Champia* sp. | | | | | S |
| *Chondria* sp. | | | | R | S |
| *Dohrniella antillarum* | | | S | | S |
| *Gelidium* spp. | D | P | D | D | D |
| *Griffithsia* sp. | | | P | | R |
| *Hypnea* sp. | S | | | | R |
| *Hypoglossum hypoglossoides* | | P | | P | |
| *Jania* spp. | P | R | P | P | D |
| *Laurencia* spp. | | | S | P | R |
| *Polysiphonia* sp. | P | D | P | D | P |
| *Taenioma* sp. | | P | | S | |
| Unid. reds | | | S | | R |
| Coeff. of Community (*CC*) | 0.495 ± 0.120 | 0.539 ± 0.109 | 0.456 ± 0.115 | 0.572 ± 0.100 | 0.535 ± 0.106 |

were pooled for the shallow reef and the gorgone zone, but not for the drop-off and reef slope, where diet selection was analyzed separately for juveniles and adults.

To investigate preference for different algal vegetation types, only those that make up a major proportion of the diet are considered. These are large turfs and macroalgae, sparse turfs on endolithic algae, sparse turfs on crustose corallines, and bare coralline crusts. Comparison of the relative occurrence of these food types in the diet to their relative abundance on the reef indicates that sparse turfs on endolithic algae are preferred on all reef zones (Table 3, Fig. 2). Large turfs are not eaten on the shallow reef, but are preferred in the gorgone zone, and the drop-off and reef slope. Bare coralline crusts and crustose corallines bearing sparse turfs are eaten to a lesser extent than would be expected if *Sparisoma viride* fed randomly on all food types.

### Preference for substrates

The occurrence of substrate types in the diets of the 3 life phases of *Sparisoma viride* was compared for each reef zone (Table 4). No significant differences in

Table 3. *Sparisoma viride*. Relative frequencies (%) of bites on different food types, and relative abundance (%) of algal food types. Within reef zones, differences in diet composition (algal food types and living corals) between life phases was tested with Chi-square. In each reef zone, relative frequency of bites on algal food types was compared to their relative abundance on the reef (Chi-square). df: degrees of freedom in statistical tests. Diet selection was analyzed separately for juveniles and adults for drop-off + reef slope zone

| Diet per reef zone<br>Life phase | Large turfs + macroalgae | Sparse turfs on endolithic algae | Sparse turfs on crustose corallines | Crustose corallines | Living corals | No. of chain-links or bites | $\chi^2_{df}$, p: among life-phases | $\chi^2_{df}$, p: available vs eaten |
|---|---|---|---|---|---|---|---|---|
| **Shallow reef** | | | | | | | | |
| Available: | 3.5 | 22.9 | 54.6 | 19.1 | – | 3802 | | |
| Eaten by: | | | | | | | | |
| Juveniles | 0.0 | 25.0 | 60.0 | 15.0 | 0.0 | 20 | $\chi^2_6 = 6.13$, | $\chi^2_3 = 37.58$, |
| Initial phase | 0.0 | 37.9 | 44.9 | 16.1 | 1.1 | 87 | p = 0.621 | p < 0.001 |
| Terminal phase | 0.0 | 47.5 | 43.7 | 7.5 | 1.3 | 80 | | |
| **Gorgone zone** | | | | | | | | |
| Available: | 13.9 | 17.4 | 57.5 | 11.2 | – | 2723 | | |
| Eaten by: | | | | | | | | |
| Juveniles | 18.8 | 39.1 | 33.4 | 8.7 | 0.0 | 69 | | |
| Initial phase | 14.4 | 32.2 | 38.1 | 13.6 | 1.7 | 118 | $\chi^2_8 = 10.27$, | $\chi^2_3 = 77.15$, |
| Terminal phase | 16.9 | 42.9 | 24.7 | 10.4 | 5.2 | 77 | p = 0.488 | p < 0.001 |
| **Drop-off + reef slope** | | | | | | | | |
| Available: | 15.9 | 8.7 | 54.7 | 20.7 | – | 5664 | | |
| Eaten by: | | | | | | | | |
| Juveniles | 35.9 | 21.9 | 39.1 | 3.1 | 0.0 | 64 | | $\chi^2_3 = 40.75$, p < 0.001 |
| Initial phase | 29.7 | 35.1 | 17.9 | 11.4 | 5.9 | 185 | $\chi^2_8 = 23.01$, | $\chi^2_3 = 282.67$, |
| Terminal phase | 26.3 | 28.0 | 26.3 | 10.2 | 9.3 | 119 | p = 0.003 | p < 0.001 |

substrate choice were found between life phases on the shallow reef and gorgone zone, and recorded bites were pooled. On the drop-off and reef slope, substrate choice of JU fish differs significantly from that of adult fish (IP and TP), and substrate selection was analyzed separately for juveniles.

When the relative occurrence of bites on different substrate types is compared with the availability of these substrates on the reef, a significant difference from random substrate choice is found in all reef zones, except for JU fish in the deeper reef zone (Table 4). In general, low-density substrates, such as *Madracis mirabilis* and *Montastrea annularis*, are preferred. Only on the drop-off and reef slope are more bites taken from high-density *Agaricia* spp. substrates. This can be attributed to differences in algal vegetation. On the drop-off and reef slope, *Montastrea annularis* forms large colonies, which support an abundant vegetation of crustose corallines (an avoided food item; see above) on the rising and tilting sides of the colonies not covered with living coral polyps. In comparison, dead *Agaricia* spp. substrates have higher cover of preferred vegetation types (large turfs and sparse turfs on endolithic algae): 30% on *Agaricia* spp. compared to 21% on *Montastrea annularis* substrates.

### Size of grazing scars in relation to food type and substrate density

Linear regression of log-transformed data showed that the surface area of bite scars is linearly related to $FL^2$. Bite scar volume is linearly related to $FL^3$. As the intercepts are not significantly different from zero, the linear regressions were forced through the origin. Regression equations of bite scar surface area (*SA*, $cm^2$) and of bite scar volume (*VO*, $cm^3$) to fish fork length (FL, cm) are:

$$SA = 5.839\ (\text{SD: } \pm 0.174) \times 10^{-4} \times FL^2; \quad r = 0.855;\ n = 414,\ p < 0.001, \tag{5}$$

and

$$VO = 1.362\ (\text{SD: } \pm 0.066) \times 10^{-6} \times FL^3; \quad r = 0.724;\ n = 393,\ p < 0.001. \tag{6}$$

One-way ANCOVA analysis shows that the surface area of grazing scars is significantly affected only by food type ($F_{(1,416)} = 14.237$, $p < 0.001$), while the volume of grazing scars is affected by food type ($F_{(1,394)} = 16.242$, $p < 0.001$) and substrate density ($F_{(1,327)} = 4.629$, $p = 0.032$). Substrate microhabitat does not significantly affect the size of grazing scars. Two-way ANCOVA, controlling for reef zone, shows that on the shallow reef zone (< 3.5 m depth) only food type significantly affects

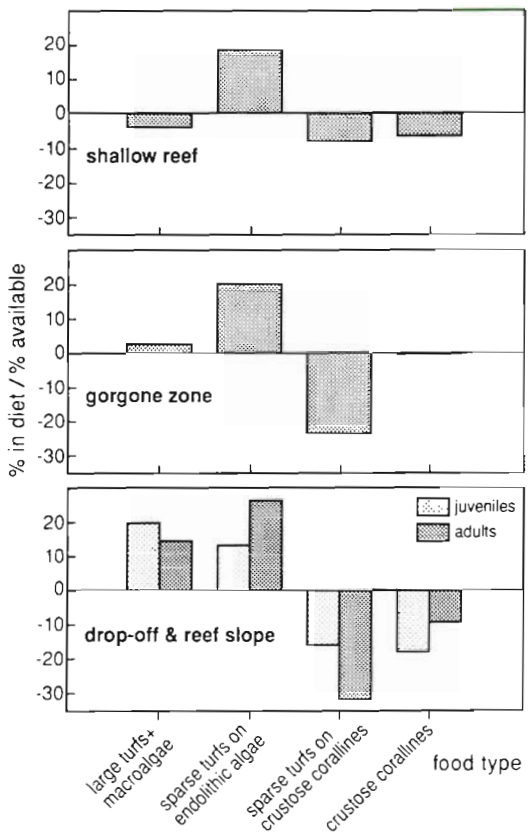



Fig. 2. *Sparisoma viride*. Food selection by stoplight parrotfish. In each reef zone, the relative occurrence of the main food types in the diet of the fish is compared to their relative abundance on the reef. Relative occurrence of available food types from Table 1; relative occurrence of food types in diet from Table 3

the surface area ($F_{(2,90)} = 14.367$, $p < 0.001$) and volume ($F_{(2,85)} = 20.172$, $p < 0.001$) of bite scars. Bites taken on substrates infested with endolithic algae result in larger grazing scars than bites taken on substrates covered with crustose corallines (Fig. 3). Although not significant, bites taken on low-density substrates generally leave larger scars than those taken on high-density substrates (Fig. 3). In deeper reef parts (> 3.5 m depth) only the skeletal density of grazing substrates significantly affects the size of bite scars (surface area: $F_{(2,151)} = 9.093$, $p = 0.003$; volume: $F_{(2,138)} = 5.457$, $p = 0.021$). Bites taken on low-density substrates result in larger grazing scars than bites taken on high-density substrates, while food type has little effect on bite size (Fig. 3).

### Foray size in relation to food type and substrate density

Foray size is positively correlated with fish size (linear regression, $r = 0.145$, $p = 0.003$). The median fork length ($FL_{med}$) and median foray size ($FS_{med}$) of the different life phases is: JU fish: $FL_{med} = 10$, $FS_{med} = 2$; IP fish: $FL_{med} = 24$, $FS_{med} = 3$; TP fish: $FL_{med} = 30$, $FS_{med} = 4$. However, within life phase categories the effect of fork length on foray size is not significant (linear regression: JU: $r = 0.001$, $p = 0.990$; IP: $r = 0.069$, $p = 0.323$; TP: $r = 0.043$, $p = 0.631$).

The distribution of total bites by foray size was investigated for each life phase separately and related to food type, substrate density and foraging depth (Fig. 4). Forays recorded on large turfs were excluded from the analysis because they are located significantly more often inside than outside territories of damselfish. The territorial defence of damselfish often interferes with feeding behaviour of other herbivores, which may result in shorter forays. The frequency distribution of total bites by foray size is significantly different between the food types tested (Fig. 4A). When grazing on sparse turfs on endolithic algae, all life phases of *Sparisoma viride* take a higher proportion of bites in long forays than when grazing on coralline crusts. The frequency distribution of bites by foray size differs significantly between high- and low-density substrates (Fig. 4B). All life phases take relatively more bites in longer forays from low- than from high-density substrates. Finally, all adult life phases grazing on the deeper reef parts (> 3.5 m depth) take a larger proportion of their bites in longer forays than fish grazing on the shallow reef (Fig. 4C). Longer forays on the deeper reef are not an effect of fish size. The mean FL of fish was not significantly different between reef zones (*t*-tests of FL between shallow and deeper reef for each life phase: $p > 0.05$).

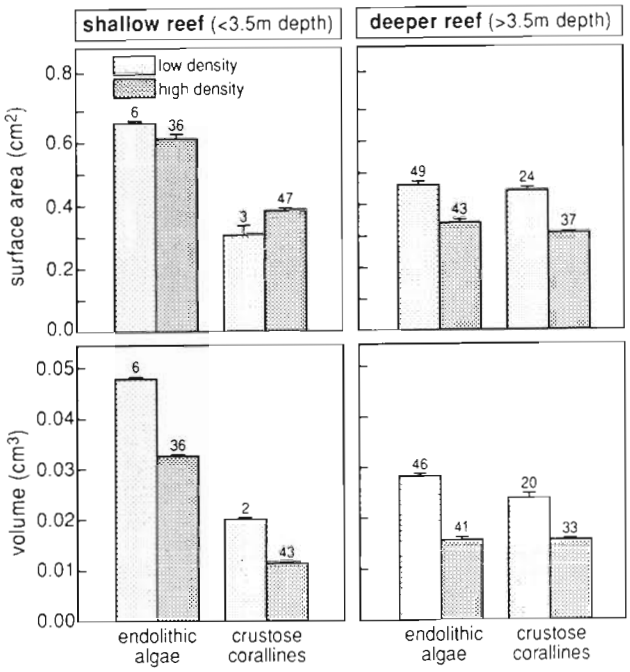
### Biochemical composition of food types

Table 5 shows biomass, protein and energy contents of the epilithic and substrate-bound fractions of the different food types. The epilithic biomass is highest for macroalgae, intermediate for large turfs, and lowest for sparse turfs. In a separate set of samples, the biomass of sparse turfs growing on endolithic algae was found to be significantly higher than that of sparse turfs on crustose corallines (Student's *t*-test, $n = 22$, $p < 0.05$). Biomass of crustose corallines, either as undergrowth of sparse turfs, or as bare crusts, is not significantly different from the biomass of endolithic algal layers. Under coralline crusts in the shallow reef, we sometimes encountered an undefined substance rich in organic components. Parrotfish grazing scars were, however, never found to penetrate into this microhabitat, and samples from this undefined layer were excluded from the analysis.

Table 4. *Sparisoma viride*. Relative frequencies (%) of bites on different dead coral substrates, compared with their relative abundance (%) on the reef. Within reef zones, differences in substrate choice between life phases were tested with Chi-square. In each reef zone, relative frequency of bites on the 3 most abundant substrate types was compared to their relative abundance of the reef (Chi-square). Substrate types are arranged along a skeletal density (g $cm^{-3}$) gradient. Substrate selection was analyzed separately for juveniles and adults for drop-off + reef slope zone

| Substrate per reef zone<br>Life phase | *Acropora cervicornis* | *Agaricia* spp. | *Acropora palmata* | *Madracis mirabilis* | *Diploria* spp. | *Montastrea annularis* | *Colpophyllia natans* | No. of chain-links or bites | ($\chi^2_4$), p: among life phases | ($\chi^2_2$), p: available vs eaten |
|---|---|---|---|---|---|---|---|---|---|---|
| Skeletal density ± SD<br>(no. of samples) | 2.06 ± 0.27<br>(4) | 1.92 ± 0.22<br>(3) | 1.77 ± 0.16<br>(3) | 1.64 ± 0.13<br>(3) | 1.57[a]<br>(?) | 1.31 ± 0.19<br>(7) | 0.86 ± 0.04<br>(3) | | | |
| **Shallow reef** | | | | | | | | | | |
| Available: | 12.8 | 0.0 | 84.4 | 0.0 | 0.6 | 2.2 | 0.0 | 3627 | | |
| Eaten by: | | | | | | | | | | |
| Juveniles | 25.0 | – | 70.0 | – | 0.0 | 5.0 | – | 20 | (3.36)<br>p = 0.500 | (43.53)<br>p < 0.001 |
| Initial phase | 11.1 | – | 77.8 | – | 0.0 | 11.1 | – | 81 | | |
| Terminal phase | 12.4 | – | 68.8 | – | 3.8 | 10.0 | – | 80 | | |
| **Gorgone zone** | | | | | | | | | | |
| Available: | 58.7 | 4.6 | 0.0 | 6.7 | 2.2 | 27.9 | 0.0 | 1671 | | |
| Eaten by: | | | | | | | | | | |
| Juveniles | 33.3 | 0.0 | – | 18.5 | 9.3 | 38.9 | – | 54 | (2.59)<br>p = 0.628 | (50.24)<br>p < 0.001 |
| Initial phase | 36.2 | 1.0 | – | 18.1 | 4.7 | 40.0 | – | 105 | | |
| Terminal phase | 38.1 | 1.5 | – | 9.5 | 6.3 | 44.4 | – | 63 | | |
| **Drop-off + reef slope** | | | | | | | | | | |
| Available: | 0.0 | 15.2 | 0.0 | 0.0 | 0.0 | 71.6 | 13.2 | 1824 | | |
| Eaten by: | | | | | | | | | | |
| Juveniles | – | 14.6 | – | – | – | 73.2 | 12.2 | 41 | | (0.97)<br>p = 0.600 |
| Initial phase | – | 38.6 | – | – | – | 47.4 | 14.0 | 114 | (10.38)<br>p < 0.050 | (69.60)<br>p < 0.001 |
| Terminal phase | – | 37.2 | – | – | – | 46.5 | 16.3 | 86 | | |

[a]From Dodge & Thomson (1974)




◀Fig. 3. Effects of food type and skeletal density of substrates on the size of grazing scars caused by *Sparisoma viride*. Food types: endolithic algae = substrates with endolithic algae bearing large or sparse turfs; crustose corallines = bare coralline crusts + coralline crusts bearing sparse turfs (see Table 3). Skeletal density categories: low density = *Colpophyllia natans*, *Diploria* spp., *Montastrea annularis* and *Madracis mirabilis*; high density = *Acropora cervicornis*, *A. palmata* and *Agaricia* spp. (see Table 4). Values (means + SE) are normalized for fish of 30 cm fork length. Value above bar indicates the number of cases

Fig. 4. *Sparisoma viride*. Effect of (A) food type, (B) substrate density, and (C) foraging depth on frequency distribution of total bites by foray size. For circumscription of categories see legend to Fig. 3. Foray sizes are grouped in 4 categories: 1 to 5, 6 to 10, 11 to 15 and 16 to 20 successive bites. Value above bar indicates the total number of bites; p indicates the level of significance of differences in frequency distributions tested with Chi-square. Asterisks indicate significant contributions of individual foray size pairs to the observed difference in frequency distribution ▼

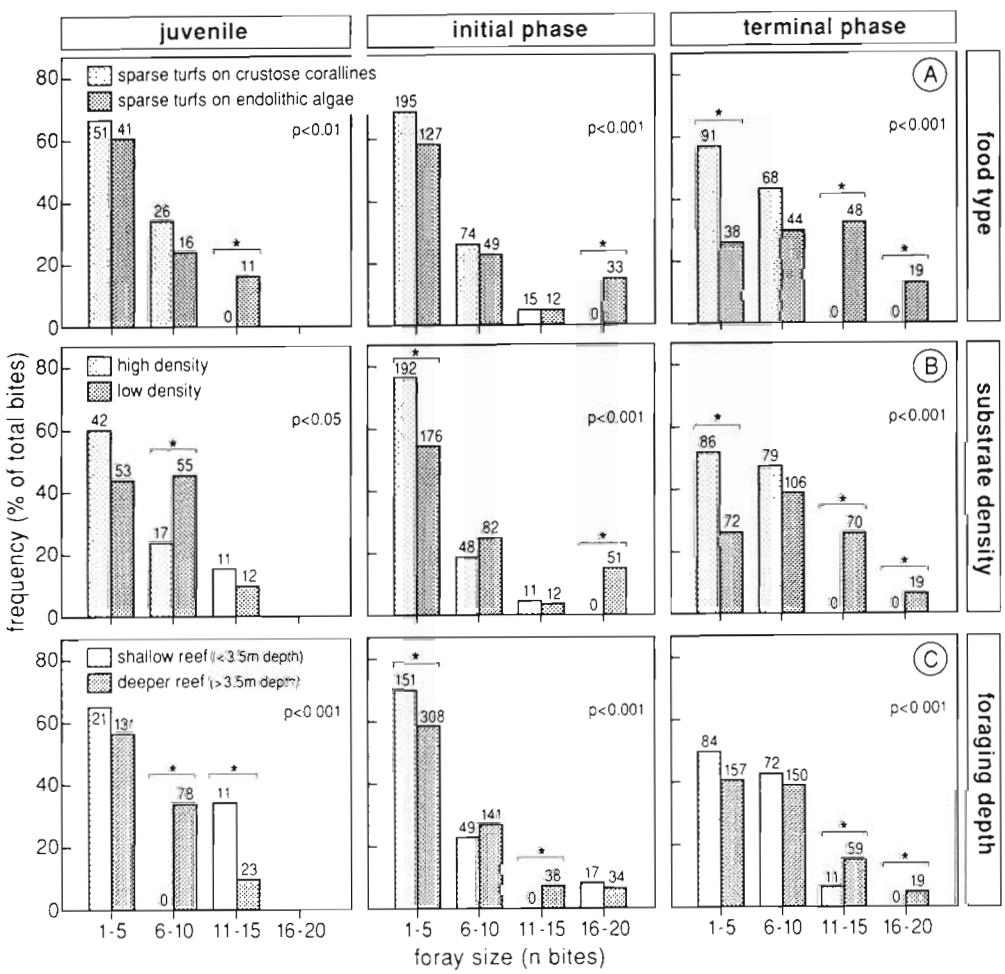


Table 5. Biochemical composition of food types. Values are means ± standard errors. n in parentheses

| Algal food types | Biomass (mg AFDW $cm^{-2}$) | Protein (mg $g^{-1}$ AFDW) | Energy (kJ $g^{-1}$ AFDW) |
|---|---|---|---|
| Macroalgae | 23.2 ± 10.2 (10) | 90.5 ± 51.2 (4) | 18.7 ± 1.5 (7) |
| Large turfs | 8.6 ± 3.7 (19) | 108.5 ± 24.5 (5) | 19.1 ± 2.0 (8) |
| Sparse turfs on: | | | |
| endolithic algae | 1.3 ± 0.1 (11) | 119.2 ± 18.6 (10) | 17.7 ± 0.2 (21) |
| crustose corallines | 0.9 ± 0.2 (11) | | |
| Endolithic algae | 17.7 ± 6.0 (58) | 94.4 ± 20.7 (6) | 23.7 ± 5.5 (7) |
| Crustose corallines | 18.6 ± 5.9 (76) | 60.2 ± 20.2 (7) | 20.0 ± 4.1 (7) |

Highest protein levels were found in sparse turfs and large turfs (Table 5). Macroalgae, on average, had lower protein levels, and especially old fronds of *Dictyota* spp. contained very little protein (36.1 mg $g^{-1}$ AFDW). Crustose corallines contained, on average, less protein than other algae.

Of the epilithic algal fractions, the energetic value of macroalgae and large turfs was higher than that of sparse turfs (Table 5). The mean energetic value of endolithic algae was higher than that of other algal food types, and crustose corallines contained more energy than did epilithic algae. Standard errors of energetic values determined for endolithic algae and crustose corallines were higher than those determined for epilithic algae.

Although not investigated systematically, no significant effect of season on the biochemical composition of algae was detected. Neither was a seasonal shift in algal biomass apparent to the naked eye.

Table 6. Yield of biomass, protein and energy per bite of different food types for *Sparisoma viride* of 30 cm fork length. Food types are ranked by yield per bite; percentage of maximum yield per bite is given in parentheses

| | Biomass (mg AFDW $bite^{-1}$) | Protein (mg $bite^{-1}$) | Energy (J $bite^{-1}$) |
|---|---|---|---|
| Large turfs | 6.83 (100) | 0.709 (100) | 141.2 (100) |
| Sparse turfs on endolithic algae | 3.00 (44) | 0.301 (42) | 67.1 (48) |
| Sparse turfs on crustose corallines | 2.22 (32) | 0.155 (22) | 43.5 (31) |
| Crustose corallines | 1.86 (27) | 0.112 (16) | 37.1 (26) |

### Yield per bite

The yield of algal biomass, protein and energy per bite was calculated for a fish of 30 cm FL (Table 6) feeding on the 4 major food types. The observed feeding preferences of *Sparisoma viride* (Table 3, Fig. 2) are correlated with the yield and quality of the food. Yields of algal biomass, protein and energy are higher from preferred food types (large and sparse turfs on endolithic algae) than from non-favoured food items (sparse turfs on crustose corallines and bare coralline crusts). Grazing on crustose corallines especially reduces the intake of protein: the percentage of the maximum attainable yield of protein per bite is lower than that of total algal biomass or energy (Table 6). This is the result of the combined effects of low protein contents and smaller size of grazing scars. On the basis of yield, however, no inferences can be made concerning the relative importance of protein and energy in determining diet choice: the ranking of the food types from highest to lowest yield per bite is the same, regardless of whether protein or energy is chosen as criterium.

## DISCUSSION AND CONCLUSIONS

### *Sparisoma viride*, a selective grazer

The diet of *Sparisoma viride* consists almost exclusively of algae associated with dead coral substrates. This corresponds well with the descriptions of the feeding habits of this herbivorous fish provided by Gygi (1975), Frydl & Stearn (1978) and Hanley (1984). Living corals are avoided as food items. Adult fish, however, take occasional bites on living corals, mainly from *Montastrea annularis* (Table 3). They create conspicuous white spots on the colonies, often located near territory boundaries. We believe these 'white spot' bites, to have a function in consolidating the social interrelationships between individuals and groups (van Rooij et al. unpubl.).

In the diet of *Sparisoma viride*, all available algal food types are represented. Except for macroalgae, the feeding pattern is non-selective with respect to algal species. Diet selection takes place on the level of algal form groups, reflecting the relatively large size of the herbivore compared to its food plants (Choat 1991).

Endolithic algae, with sparse or large turfs, are a preferred food resource, while crustose corallines, with or without algal turfs, are eaten more or less proportionally to their overall occurrence on the reef.

The observed food preference will be discussed in relation to the nutritional quality of the algal-form groups and their yield. The social organization of *Sparisoma viride* will be examined in relation to the availability of preferred food types in the different reef zones.

### Nutritional quality

*Sparisoma viride* grows continuously throughout its life (J. M. van Rooij, J. H. Bruggemann & J. J. Videler unpubl.), and engages in reproductive activities on a daily basis throughout the year (Bruggemann pers. obs.). These activities suggest that protein and energy may constrain individual performance. This is borne out by the observation that *S. viride* prefers to feed on those food types containing the highest levels of protein (sparse turfs growing on endolithic algae) or energy (large turfs on endolithic algae). An anecdotal observation may illustrate the critical importance of protein and energy in the diet. The macroalga *Lobophora variegata*, rich in protein and energy (166.1 mg $g^{-1}$ AFDW and 19.8 kJ $g^{-1}$ AFDW respectively), grows below the lower limits of the foraging areas of territorial *S. viride*. In 2 territories, the TP males were repeatedly observed to leave their always fiercely defended areas, and make quick foraging excursions to the deeper growing *L. variegata* stands. These excursions were made at regular intervals, and during each excursion a few bites were taken exclusively on *L. variegata*.

Additional sources of protein in the form of animal food products may be ingested intentionally or inadvertently. Based on the presence of numerous remains of crustaceans, copepods and sponges in the faeces of small JU *Sparisoma viride* (< 10 cm FL), we conclude that these fish supplement their algal diet with animal food products (pers. obs). Carnivory in juvenile scarids was also described by Bellwood (1988). Although sparse turfs contain more protein than large turfs and macroalgae, protein intake from the latter food type could be augmented by the accidental ingestion of small invertebrates living between the algal fronds. The contribution of these animal food products to the daily nutrient and energy intake by this herbivorous fish was, however, not quantified.

The energetic values of epilithic algal turfs and of macroalgae fall within the range of values previously reported by Cummins & Wuycheck (1971) and Dawes (1986), but are somewhat higher than those determined by Paine & Vadas (1969), Montgomery & Gerking (1980) and Fris & Horn (1993). In all these studies direct calorimetry was used. However, as most of our samples contained over 80 % $CaCO_3$, it was impossible to obtain reliable estimates of their bomb caloric values by direct measurements (Paine 1966). The energetic values for marine algae, as calculated by Gnaiger & Bitterlich (1984) from elemental analysis, are similar to our own results.

Macroalgae had higher energy content than other epilithic algae (Table 6). In the feeding ranges of *Sparisoma viride*, macroalgae are represented mainly by Pheophyta (i.e. *Dictyota* spp.), while large and sparse turfs mainly consist of representatives of the Rhodophyta. Montgomery & Gerking (1980) also found brown algae to have higher energy contents than red algae. Endolithic algae appear to be an energy-rich food resource, which can be attributed to the blue-green and green algae that predominate in this vegetation type (Golubic et al. 1975). Cyanobacteria have murein cell walls that contain an energy-rich lipopolysaccharide layer (van den Hoek 1978). Other authors (Cummins & Wycheck 1971, Montgomery & Gerking 1980, Dawes 1986) also reported higher energetic values for green and blue-green algae than either brown or red algae. Energetic values for crustose corallines were higher than those determined by Paine & Vadas (1969), which may be the result of differences in analytical methods. Finally, a cautionary remark concerning the energetic values of the substrate-bound algal fractions should be made here. The elemental CN analysis of endolithic and crustose coralline algae yielded more variable results than analysis of the epilithic algal fractions, as indicated by relatively high standard errors. It is conceivable that in some samples, not all inorganic C was completely removed, even after prolonged acidification with $H_2SO_3$. Residual inorganic C results in erroneously high carbon contents, and in overestimation of true energetic value. In particular, samples that contain large amounts of crystalline calcium carbonate, such as the substrate-bound algal fractions, are prone to this type of error.

### Yield as basis for food selection

Our estimates of yield were made under the assumption that all material bitten off was also ingested by the fish. Spilling of material that was scraped off but not ingested was occasionally observed in the field. Sometimes the entire potential food mass was spit out, which occurred mainly when bites were taken from living corals. However, sloppy feeding was observed in only a minority of bites and we have no indication that some food items (except living corals) were rejected more frequently than others.

*Sparisoma viride* employs an excavating feeding mode, and leaves deep grazing scars on limestone substrates (Gygi 1975, Frydl & Stearn 1978). This means that a large proportion of its diet consists of endolithic and crustose algae. The relative yield of the substrate-bound component clearly contributes to the observed feeding preferences. As grazing scars on the preferred endolithic algae are generally larger those on the avoided crustose corallines (Fig. 3), this implies a lower yield per bite of the latter food type. Although the predominant carbonate mineral in crustose corallines (magnesium calcite: hardness = 3) is 'softer' than the carbonate mineral of coral substrates (aragonite: hardness = 3.5 to 4) (Deer et al. 1966), grazing scars on the latter are bigger than those on crustose corallines. This is due to weakening of the carbonate matrix by the boring action of endolithic green and blue-green algae (Golubic et al. 1975).

Substrate density also affects the amount of substrate that *Sparisoma viride* can excavate per bite: low-density substrates enable deeper bites, and higher yields of endolithic algae, than high-density substrates (Fig. 3). The assimilation efficiency of algal food is also dependent on substrate type. Bruggemann et al. (1994, in this issue) showed that fish grazing from low-density *Montastrea annularis* substrates attained higher assimilation efficiencies than fish that were fed high-density *Acropora* spp. substrates, resulting in a higher net yield. In general *S. viride* showed significant preference for low-density substrates. On the drop-off and reef slope, low-density dead *M. annularis* and *Colpophyllia natans* colonies constitute over 85% of the grazing surfaces accessible to herbivorous fish. In contrast, the dominant substrate types found on the shallow reef and gorgone zone are high-density *Acropora* spp. corals (Table 4). Resulting from this distribution of substrate types over the reef, *S. viride* grazing on the drop-off and reef slope will attain on average higher yields per bite than congeners grazing in shallower parts of the reef (Bruggemann et al. 1994).

### Foray size as indication of feeding preference and food patch quality

Diet selection in animals is often explained from the premise that they strive to maximize their energy or specific nutrient intake per unit foraging time and/or effort (Stephens & Krebs 1986). Thus, foray size is an indication of food preference, independent of comparisons between diet composition and available resources. All life phases of *Sparisoma viride* took longer forays on food and substrate types that enable the highest yields per bite (sparse turfs on endolithic algae and low-density substrates) (Fig. 4A, B). Taking more successive bites on high-yield food types once they are located and access to them is gained increases food intake per unit time and effort. This is a profitable strategy in an environment full of competitors.

### Limitations to food selection: availability of food types

In spite of selective grazing, a large proportion of the diet of *Sparisoma viride* consists of inferior food items. This raises the question whether diet selection is limited by the availability of preferred food types. To evaluate this question, the relative abundance of the food types should be related to the density of their consumers. The density of herbivorous fish (Scaridae, Acanthuridae and Pomacentridae) decreases along a depth gradient, from 21.9 kg fish wet wt (FWW) 100 $m^{-2}$ on the shallow reef to 3.3 kg FWW 100 $m^{-2}$ on the drop-off and reef slope (Bruggemann unpubl. results). When only the parrotfish *S. viride* is considered, the population density on the shallow reef is still more than 5 times higher than that on the drop-off and reef slope (3.3 and 0.6 kg FWW 100 $m^{-2}$ respectively). This means that the algal resources on the shallow reef are shared among many more consumers than in the deeper reef.

On the shallow reef, all life phases of *Sparisoma viride* spend over 90% of the day feeding. The high foraging effort is probably indicative of limited food resources. More than 50% of all bites recorded on the shallow reef were taken on inferior food types, i.e. crustose corallines, with or without algal turfs. Grazing on these food types decreases with depth, although it still accounts for ca 30 to 40% of bites on the drop-off and reef slope (Table 3). Reduced competition for high quality food, resulting from lower herbivore densities, can explain these differences in diet composition between reef zones.

### Territorial behaviour in relation to food quality and availability

Territoriality can only arise where a stable, rich food supply can be economically defended, a principle illustrated in terrestrial systems (Horn 1968) as well as in the marine environment (Barlow 1974, Vine 1974). For *Sparisoma viride*, the favourable food resources are not distributed evenly over the reef. The abundance of high-yield food patches consisting of large turfs and macroalgae growing on low-density substrates is higher on the drop-off and reef slope than in the shallow reef (Tables 3 & 4). Also the accessibility of preferred food types is higher on the deeper reef parts,

as indicated by the changes in diet composition in relation to foraging depth. At the study site, both territorial and non-territorial behaviour is found in *S. viride*. The increased abundance at greater depth of the high-yield food and substrate types coincides with the occurrence of haremic territories of *S. viride*. The daily number of bites taken is lower for fish feeding inside these territories than for fish grazing on the shallow reef (outside territories) (Bruggemann et al. 1994). Similarly, the part of the daily active period spent on feeding is lower for territorial *S. viride* (ca 70%) than for non-territorial fish (>90%). However, the lower foraging effort does not result in lower daily food intake by territorial *S. viride* (Bruggemann et al. 1994), because of higher yields per bite. Thus, with lower foraging effort, territorial fish attain a daily food intake that is similar to that of non-territorial conspecifics. The social organization of *S. viride* at Karpata seems to illustrate the principle of territoriality arising where a stable high-quality food supply can be economically defended.

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